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REVIEW ARTICLE

A review of environmental and anthropogenic variables used to model jaguar occurrence

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Abstract
Jaguars (*Panthera onca*) are a landscape species of conservation importance and our understanding of environmental and anthropogenic drivers of jaguar occurrence is necessary to improve conservation strategies. We reviewed available literature to simply describe environmental and anthropogenic variables used and found to be significant in occurrence modeling. We reviewed 95 documents published from 1980 to 2021 that focused on jaguar occurrence and that used 39 variable types (21 anthropogenic, 18 environmental) among different techniques, scales, and approaches. In general, these variables included both anthropogenic (roads, land use, human activities, and population) and environmental (climate, vegetation, ecological interactions, topographic, water, and others) factors. Twelve variables were identified as affecting jaguar occurrence overall, eleven at local scale and seven at broad scales (regional and continental). Focusing more specifically on the variables that correlate with occurrence should help researchers to make better predictions in areas without quantitative jaguar data.

Keywords
habitat, humans, landscapes, *Panthera onca*, prey, roads

PENSOFT.

Introduction

Understanding drivers of species distribution under global change scenarios, whether directly anthropogenic or indirectly climatic, is crucial for the development of nature conservation strategies (Kareiva and Marvier 2015). More specifically, resource abundance should determine potential species abundance and distribution, and direct mortality factors should constrain species occurrence (Manly et al. 2002). Thus, documenting and understanding how environmental and anthropogenic factors allow/limit species distribution is essential for species conservation (Morrison et al. 2006; Paschoaletto and De Barros Ferraz 2012).

There are different approaches and interpretations to estimating species distribution, and selection of proper state variables that have causal effects may influence inferences over time and space (Mackenzie and Nichols 2004; Mackenzie et al. 2017). Similarly, the ways in which data are collected (methods and techniques), scale considerations (from fine to broad scale), and statistical approaches (analysis and extrapolation techniques) also may influence findings and predictions. Nevertheless, there often is a lack of systematic classification of common environmental and anthropogenic factors related to species modeling approaches.

Populations of jaguars (*Panthera onca*), the largest felid on the American continent (Seymour 1989), have been gradually extirpated (Ceballos et al. 2005; Ripple et al. 2015) and now occur in only 54% of their historic geographic range (Sanderson et al. 2002). The species is classified as "Near threatened" (Quigley et al. 2017) and previous jaguar population assessments at the continental scale also show a continued rate of decline (Rabinowitz and Zeller 2010; De la Torre et al. 2017) due to trophy hunting, killing as retaliation by livestock predation, habitat loss, human expansion, and poaching of prey (Quigley et al. 2017). Jaguars are landscape species with large home ranges extending beyond protected areas and across a variety of ecosystems under a gradient of anthropogenic pressures (Silver et al. 2004; Thornton et al. 2016). As apex predators they functionally maintain ecosystem balance and structure, regulating populations at lower trophic levels to more stable states (Estes et al. 2011; MacBride and Thompson 2018; Thompson et al. 2020). Studying free-ranging jaguars can be logistically demanding and expensive due to their elusive behavior, large home range sizes, and low population densities, often in places that are isolated and difficult to access (Salom et al. 2007; Carrillo et al. 2009). As a result, jaguar occurrence across the Americas is fairly well known (Rabinowitz and Nottingham 1986; Rabinowitz and Zeller 2010), but questions about their more precise occurrence trends at different scales, and particularly factors directly influencing distribution, are still relevant as research priorities (Sanderson et al. 2002; De la Torre et al. 2017; Sanderson et al. 2022).

Here we summarize and examine the most-used anthropogenic and environmental predictor variables, and modeling and data collection approaches, cited in peer reviewed literature that best described jaguar occurrence. If a relatively small number of factors were consistently identified as important, then the need for additional such studies would be less. The outcome of this assessment should allow

the reconsideration of meaningful (and meaningless) predictor variables in future modeling of jaguar occurrence, and thus make the future application of model results more useful and successful.

Materials and methods

A comprehensive literature review of factors influencing jaguar distribution was conducted using two Internet search engines (Web of Science and Google Scholar). A systematic search was temporally delimited from 1980 to 2021 and used the following combination of words: "Jaguar" + "Distribution" + "Environmental variables" + "Prey abundance" + "*Panthera*" + "Occurrence". For each publication identified as relevant, we identified the methods of analysis used to inform jaguar occurrence, the geographic scale of the assessment, and a list of variables included in the assessment. We sort the data gathering methods into seven categories: telemetry, camera trap, genetics, historic records, sign counts, interviews, and data derived from geographic information systems (GIS). The analysis methods were separated into four categories: Occupancy (specific modeling approach base on the proportion of areas or sample units occupied), Niche modeling (species-distribution models that used presence data to infer ecological requirements to elucidate potential distributions), deductive (base on previous knowledge and species-environment associations from expert opinion to envisage distribution), and basic statistical empirical approaches (included a number of methods such as comparison tests, generalized lineal models, and analysis of covariance). We also classified the range extent of each study into four scale categories: continental, regional, country, and local. Similar variables with different names were classified into one-name variables, and these were subsequently sorted into sub-categories within the broader categories of anthropogenic and environmental factors in a Microsoft Excel spreadsheet (Suppl. materials 1, 2).

Once we collected the entire range of predictor variables of jaguar occurrence, we identified those that were reported as having a statistically significant influence on occurrence/distribution. We assessed which were most identified, and the degree to which these were related to geographic scale.

Results

We identified 165 peer reviewed documents in our search, but only 95 either tackled issues of jaguar distribution or correlated distribution with anthropogenic or environmental factors. Among these studies we found that the number of jaguar distribution studies recently has increased, with almost 98% of the literature being published after 2000 (Fig. 1A). Most studies took place in Brazil (n = 28), Mexico (n= 16), and Belize (n = 10; Fig. 1B).

Among the studies there were four main modeling approaches (Table 1). The most widely used were basic statistic empirical models (n = 41; Suppl. material 1) which usually analyze or describe summaries of empirical data based on correlation among variables (Morrison et al. 2006). Niche or presence-only models (n = 22)

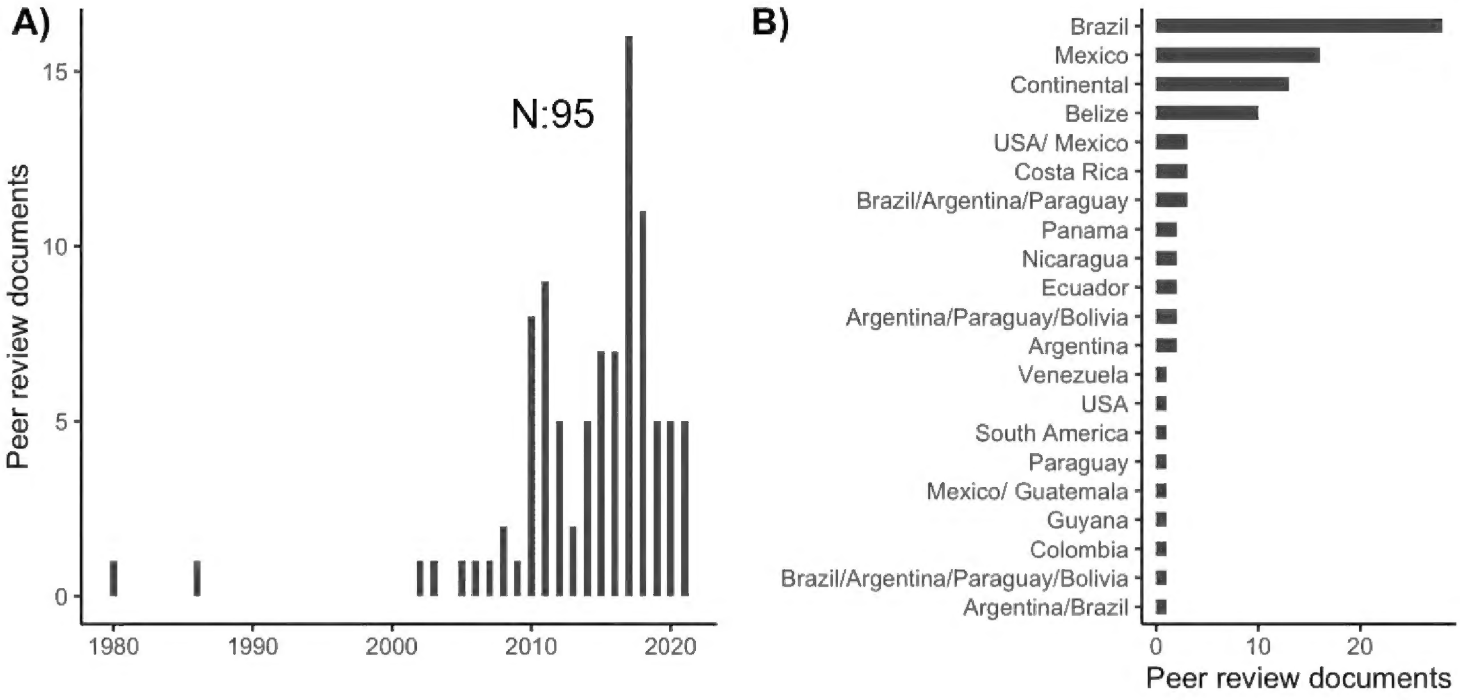

Figure 1. A Annual number of peer-reviewed documents, and **B** country(region)-specific number of peer reviewed documents assessing distribution of jaguars.

Table 1. Frequency of modeling approaches, data gathering methods, and geographic scale used to assess jaguar occurrence, as tabulated from a review of 95 peer-reviewed papers published between 1980 and 2021 (Suppl. material 1).

Research topic	Model method	No. of references	Perc. of references
Data type	Telemetry	16	17
	Camera trap	38	40
	Genetics	3	3
	Historic records	21	22
	Sign counts	2	2
	Interviews	3	3
	GIS	12	13
Modeling approach	Occupancy	20	21
	Niche modeling	22	23
	Deductive	12	13
	Basic statistic empirical models	41	43
Geographic scale	Continental	13	14
	Regional	12	13
	Country	8	8
	Local	62	65

rely on occurrence records together with environmental variables to represent the ecological-niche of a species (Phillips et al. 2017). Occupancy models (n = 20) use detection/no-detection records with a set of different covariates combination to choose the best models that explain species occupancy across the sites (Mackenzie et al. 2017). Deductive approaches (n = 12) rely on previous knowledge of species-habitat relationships based on literature or expert opinion (Morrison et al. 2006).

A variety of research techniques used to gather data for assessments of jaguar distribution (Table 1; Suppl. material 1). Data from camera trapping was used most often (n = 38), but historic records (n = 21), telemetry studies (n = 16), and data

derived from geographic information systems (GIS; n = 12) were also commonly relied on. Data from sign counts, interviews and genetic studies were used less often.

There also were multiple geographic scales used in modeling efforts (Table 1). Most were local or study area-specific (n = 62), but a number of papers assessed jaguar distribution at continental (n = 13), regional (n = 12), or country (n = 8) scales.

Our summation of different qualitative and quantitative variables types used to model jaguar distribution identified a total of 39, including 21 classified as anthropogenic and 18 as environmental (Table 2). The anthropogenic variables were sorted into four subcategories: road, land use, human activities, and population. Environmental variables were sorted into six subcategories: climatic, vegetation, wildlife, topographic, water, and other.

Anthropogenic variables

Anthropogenic variables were often described as significant groups of variables negatively affecting jaguar presence as a result of human infrastructure, population growth, and human behaviors (e.g., Silveira et al. 2014; Montanarin 2020; Palmeirim and Gibson 2021). Within subcategories, 28–53% of studies including such variables reported at least one as important affecting jaguar distribution (Table 2).

Roads have been identified as having a direct effect on jaguar habitat quality, increasing fragmentation and access to pristine areas (Hatten et al. 2003; Colchero et al. 2010; Espinosa et al. 2018; Gese et al. 2018; Romero-Muñoz et al. 2018; Cobucci-Cerqueira et al. 2021), increasing poaching of jaguars and prey (Sanderson et al. 2002), as well as stressing animals' behavior near highly used roads (Petracca 2010). Studies we reviewed incorporated three "road" metrics in models: distance to roads, road density, and distance to railroads (Table 3). Nevertheless only 8 (28%) of the 29 papers that used road variables reported statistical evidence (Table 2), distance

Table 2. Proportion of qualitative and quantitative subcategories including variables identified as significant in affecting jaguar distribution, as classified in an assessment of peer-reviewed documents published during 1980-2021 (n = 95).

		References with >1 variable		
Subcategory	**Subcategory**	**No. of variables in each subcategory[a]**	**No.**	**Percent with ≥1 significant variable**
Anthropogenic	Road	3	8	28
	Land use	3	13	41
	Human activities	11	25	53
	Human population	4	14	33
Environmental	Climatic	3	14	34
	Vegetation	6	37	53
	Wildlife	2	39	72
	Topographic	2	14	32
	Water	2	10	24
	Others	3	1	25

[a] See Table 3 for list of variables.

Table 3. Proportion of qualitative and quantitative variable types as significant in affecting jaguar occurrence, as classified in an assessment of peer-reviewed documents (n = 95) published during 1980-2021 (Suppl. materials 1, 2).

Category	Subcategory	No. of documents	Variable	Papers with variable	
				No.	Percent significant
Anthropogenic	Roads	29	distance to roads	27	26
			road density	1	0
			distance to railroads	1	0
	Land use	32	land cover type	29	41
			distance to forest	1	100
			distance to agriculture	2	0
	Human activities	47	level of area protection	9	56
			distance to protected areas	9	56
			cattle density	9	44
			human activities	6	33
			hunting pressure	6	67
			forest loss	1	100
			human footprint	2	50
			distance to tourism	1	100
			number of dams	2	50
			fires	1	0
			indigenous communities nearby	1	0
	Human population	43	distance to settlements	24	21
			population density	16	44
			number of houses	1	100
			Settlements	1	0
Environmental	Climate	42	seasonality	13	31
			precipitation	16	38
			temperature	13	31
	Vegetation	70	vegetation type	56	59
			connectivity	3	0
			ecosystem type	3	33
			NDVI	4	25
			tree richness	1	0
			primary production	3	67
	Wildlife	54	prey occurrence/abundance	27	85
			conspecifics occurrence/abundance	27	59
	Topographic	44	elevation	30	43
			slope	14	7
	Water	41	distance to water	38	24
			runoff	3	33
	Other	4	distance to the beach	1	100
			soil type	2	0
			geology	1	0

to roads being the most common and only significant metric (significant in only 7 [26%] of 27 papers; Table 3).

Land use variables often are considered to reflect restriction of jaguar distribution by reducing the resources available for populations in the wild, thus

representing a source of perturbation (Cuyckens et al. 2017). Reviewed papers included land cover, distance to forest, and distance to agriculture as modeled variables (Table 3), and 13 (41%) of 32 papers that assessed land use variables reported significant correlation patterns involving land cover (Table 2). Land cover type was the most common metric used, but only identified as significant in 41% of the 29 references in which it was included (Table 3). Distance to forest (n = 1) and distance to agriculture (n = 2) were rarely included in models, and only distance to forest was identified as significant.

Human activities are kinds of economic, recreational, or illegal activities carried out by humans that directly affect jaguar presence or biological processes within jaguar range (Carvalho et al. 2015; Jordan et al. 2016; Jędrzejewski et al. 2017; Silva et al. 2018; Ávila-Nájera et al. 2019; Ávila-Nájera et al. 2020). For such human activities 11 metrics were identified, including level of protection, distance to protected areas, cattle density, human activities, hunting pressure, forest loss, human footprint, distance to tourism, number of dams, fires, and indigenous communities nearby (Table 3). For these variables, 25 (53%) of 47 papers that assessed human activities reported significant influences (Table 2). Each human activity variable was used in only 1 to 9 models, but those used in at least 2 models were identified as significant by 50–67% of them (Table 3).

Human population variables synergistically interact with other factors magnifying the impact of human activities on jaguar distribution (Jędrzejewski et al. 2018). Of the four metrics identified in the 14 (33%) of 43 papers that included human population variables, human population density was significant in 44% of 16 papers, and distance to settlements in only 5 (21%) of 24 papers (Table 3).

Environmental variables

Environmental drivers of species distribution mostly relate to biotic and abiotic factors essential for species survival (e.g., Ashcroft et al. 2011; Gonzales-Borrajo et al. 2019). Climate variables are widely used to model distribution, especially at macro-scales, and directly affect seasonal variation resource abundance, thus forcing organisms to move (Astete et al. 2017a; Gese et al. 2018). Three climate metrics were included in 42 papers (seasonality, precipitation, and temperature), but only 14 papers (33%) identified any of them as being significantly correlated with jaguar occurrence (Table 2). Individual variables incorporated into 13–16 papers each only were identified as significant in 31–38% (Table 3; Suppl. material 1).

For jaguars, vegetation can serve as a refuge for resting and reproduction, but also can reflect both the distribution of prey and cover necessary for successful hunting (Zeilhofer et al. 2014; Booker 2016; Dobbins et al. 2017; Souza et al. 2017; Thompson and Velilla 2017; De la Torre and Rivero 2019). Of the six vegetation-related variables considered in models (ecosystem type, connectivity, vegetation type, normalized difference vegetation index [NDVI], tree richness, and primary production), 37 (53%) of 70 papers assessing vegetation reported significant correlations

(Table 2). Vegetation type was the only variable used in >3 models and was identified as significant in most (53%) of those.

Wildlife variables focus on available prey resources and potential competitors (Schaller and Crashaw 1980; Conde et al. 2010; Astete et al. 2017b; Hidalgo-Mihart et al. 2018). Both the prey and/or conspecific occurrence/abundance variables were identified as significantly influencing jaguar distribution in 39 (72%) of 54 papers including these ecological interactions. In addition, both variables were identified as significant in the majority (85 and 59%) of models in which they were assessed (Table 3; Suppl. material 1).

Topographic variables derived from terrain structure relate to general habitat associations, therefore defining local species distribution (e.g., Punchi-Manage et al. 2013). Jaguar distribution studies use a variety of such metrics (i.e., average elevation, altitude, roughness) that we pooled into a single elevation variable category, but slope was also a commonly used variable. Nevertheless, only 14 (32%) of the 44 papers reported significant correlations with jaguar distribution, elevation being the most common and most significant (43%; Table 3).

Water is a crucial resource for wildlife; it shapes ecosystem and community dynamics (e.g., Sirot et al. 2016), and often affects the temporal distribution of both jaguars and their prey (e.g., Cavalcanti 2008). In the 41 papers incorporating distance to water (and twice runoff) into models, only 10 (24%) reported significant correlation with jaguar distribution and this was most true for studies in seasonal ecosystems.

Two studies incorporated three other variables into models (soil, geology, and distance to the beach) of which only distance to beach was once identified as a significant metric in explaining jaguar occurrence (Table 3).

Variable significance at different scales

Only one variable (vegetation type) was assessed in more than half of the documents (Table 3), and ten variables used were reported as not significantly correlating with jaguar occurrence. Of the remaining 27 "significant" variables we identified the set of 12 variables as the most important in explaining jaguar occurrence (Table 4). These included vegetation type (n = 33), prey (n = 23), conspecifics (n = 16), elevation (n = 13), landcover type (n = 12), distance to water (n = 9), distance to roads (n = 7), population density (n = 7), precipitation (n = 6), distance to protected areas (n = 5), level of protection (n = 5), and distance to settlements (n = 5). With regard to the variable importance at different scales, we identified that most studies at local scale reported 11 significant variables within this selection of best predictors, with the exception of human population density at the regional and continental scale (Table 4). At broad scales such as regional and continental level, we identified as best predictors vegetation type, landcover type, distance to roads, population density, precipitation, level of protection, and prey as the most important (Table 4).

Table 4. Qualitative and quantitative variable types as significant in affecting jaguar occurrence, at multiple scales (Continental, Regional, Country, Local) classified in an assessment of peer-reviewed documents (n = 95) published during 1980-2021 (Suppl. materials 1, 2).

Category	Subcategory (n)	Variable cont.	No. of significant variables			
			Cont.	Reg.	Coun.	Loc.
Anthropogenic	Roads (29)	distance to roads	1	3	0	3
		road density	0	0	0	0
		distance to railroads	0	0	0	0
	Land use (32)	land cover type	1	3	2	6
		distance to forest	0	0	0	1
		distance to agriculture	0	0	0	0
	Human activities (47)	level of area protection	1	0	1	3
		distance to protected areas	0	0	0	5
		cattle density	0	0	1	3
		human activities	0	0	0	2
		hunting pressure	1	2	0	1
		forest loss	0	0	0	1
		human footprint	0	0	0	1
		distance to tourism	0	0	0	1
		number of dams	1	0	0	0
		fires	0	0	0	0
		indigenous communities nearby	0	0	0	0
	Human population (43)	distance to settlements	0	0	2	3
		population density	2	3	1	1
		number of houses	0	0	0	1
		settlements	0	0	0	0
Environmental	Climate (42)	seasonality	0	0	0	4
		precipitation	1	1	1	3
		temperature	1	1	0	2
	Vegetation (70)	vegetation type	2	6	4	21
		connectivity	0	0	0	0
		ecosystem type	0	0	1	0
		NDVI	0	1	0	0
		tree richness	0	0	0	0
		primary production	2	0	0	0
	Wildlife (54)	prey occurrence/abundance	1	1	1	20
		conspecifics occurrence/abundance	1	2	1	12
	Topographic (44)	elevation	0	2	1	10
		slope	0	1	0	0
	Water (41)	distance to water	0	0	0	9
		runoff	0	0	0	1
	Other (4)	distance to the beach	0	0	0	1
		soil type	0	0	0	0
		geology	0	0	0	0

Discussion

Early jaguar distribution research was limited by available techniques and technologies, making it difficult to understand important influential variables. With the development of techniques such as camera trapping in India for tigers (*Panthera tigris*)

(Karanth 1995), its use for informing jaguar distribution in the Americas (Silver et al. 2004) increased. Reliable and satellite telemetry equipment furthered research capacity (e.g., Morato et al. 2016). Also, the development of higher computer hardware capacity led to increasingly sophisticated analysis techniques, such as deductive GIS modeling (Sanderson et al. 2002; Zárrate-Charry et al. 2018; Craighead et al. 2019), occupancy modeling (Mackenzie et al. 2017), and niche modeling (Phillips et al. 2017), that has accelerated the efficiency with which jaguar data of various kinds have been used to provide insights into jaguar distribution.

Occurrence model reliability likely is affected by scale, survey technique used, and the anthropogenic and environmental metrics available to be included (Boydston and Gonzàles 2005; Torres et al. 2008; Bitetti et al. 2010; Sollmann 2011; Sollmann 2012; De la Torre et al. 2017; Gese et al. 2018). Most of the studies we surveyed were conducted at a local scale and utilized precise data mostly from camera trap surveys (Michalski et al. 2015; Watkins et al. 2015; Fort 2016; Jordan et al. 2016; Astete et al. 2017a). Nevertheless, local-scale camera-trap modeling studies, for example, may sometimes have scale mismatch issues because they only have available coarse, countrywide geographical layers to apply to ecological processes evaluated at fine scale (e.g., Quiñones et al. 2018); this is a common issue across modeling approaches independent of particular taxa (MacGarigal et al. 2016). Also, camera traps do not capture location information when jaguars or other species are resting, but those places might also be important determinants of distribution and density.

Relevant evidence of road-based metrics affecting jaguar distribution were observed in a few studies (Colchero et al. 2010; Torres et al. 2012; Zeilhofer et al. 2014; Borrego 2015; Dueñas-López et al. 2015; DeMatteo et al. 2017), presumably as consequence of better access routes that result in increased poaching (Sanderson et al. 2002; Petracca 2010). Distance to roads was a common metric in reviewed documents, perhaps because this variable can be easily built with any basic GIS (geographic information system) software (DeMatteo et al. 2017; Gese et al. 2018), but when included it most often was not identified as a significant variable.

Land use metrics should reflect both exposure to negative human interactions and a limitation of prey resources (Junior et al. 2013; Cuyckens et al. 2017). Land cover was identified as a significant metric in many, but not a majority, of studies in which it was assessed, but showed discrepancies in terms of pixel resolution across the studies (Zeller and Rabinowitz 2011; Cuervo-Robayo and Monroy-Vilchis 2012; Cullen et al. 2013; Morato et al. 2014; Torres 2021). Though additional exploratory correlation of urban development and jaguar density was not the most significant, this may be because most jaguar distribution studies used national or global land cover layers due to the high expenses incurred getting higher resolution data at local scale (Hansen et al. 2013).

Human activities may affect jaguar presence or biological processes as a result of anthropogenic recreation or economic activities, including poaching or hunting of jaguars and their prey (Sandoval et al. 2011; Jordan et al. 2016; Jędrzejewski et al. 2017; Silva et al. 2018; Portugal et al. 2019). The metrics of distance to protected

areas and level of protection were significant in only half of the studies where they were assessed, and though these two metrics can be easily built, they do not always reflect the intensity and efficiency in law enforcement which we assume to contribute importantly to wildlife occurrence. Also, hunting pressure was identified as significant in 2 or 3 studies, and though this makes clear sense, it is a variable that is difficult to adequately measure and map.

Metrics identified in the population subcategory such as human population density and distance to settlements were sometimes identified as significant, perhaps magnifying the importance of other factors assessed but also indicating that jaguars can co-exist adjacent to areas where people, and perhaps particularly livestock owners, live (Jędrzejewski et al. 2018).

Environmental variables were widely used and mostly described biotic and abiotic factors essential for species subsistence (Ashcroft et al. 2011; Luja et al. 2017; Thompson et al. 2021). Within the subgroups of variables, it seems likely that some metrics are autocorrelated. For example, the climate group variables of seasonality, precipitation, and temperature were all significant in some studies, but seasonality is influenced by the interaction of precipitation and temperature, where high temperatures and low precipitation increase droughts that may also increase mortality because when a drought comes, it also diminishes available food (Sirot et al. 2016). Given the jaguar's wide geographic distribution encompassing many different biome types, it is not surprising that their occurrence is not strictly dictated by a specific climate regime, and inclusion of such variables in local occurrence modeling may not be necessary.

Vegetation variables were the most used across jaguar studies (Sanderson et al. 2002; Weckel et al. 2006), vegetation type being significant in most. Vegetation type may represent refuge (similar to a forested land cover metric, or an inverse to anthropogenic land cover), a source of prey, and stalking or hunting habitat (Zeilhofer et al. 2014; Booker 2016; Olsoy et al. 2016; Dobbins et al. 2017; Souza et al. 2017).

Wildlife interactions, when they can be identified and mapped, are both common and highly significant factors influencing jaguar distribution. Prey occurrence and abundance are important to jaguars not only because of their high demand relative to other mammals (Sunquist and Sunquist 2002; Guilder et al. 2015), but also because prey has such an influence on carnivore demography (Fuller and Sievert 2001). In places with high prey availability jaguar density is positively correlated as López and Miller (2002) hypothesized. Both prey and competing predator distribution and abundance are often simultaneously collected using camera traps, and are thus both available and reasonable metrics to include in models (Weckel et al. 2006; Azevedo and Murray 2007; Harmsen et al. 2009; Davis et al. 2010; Petracca 2010; Harmsen et al. 2011; Rodríguez-Soto et al. 2011; Petracca et al. 2013; Arroyo-Arce et al. 2014; Gutiérrez-González and López-González 2017; Dallas and Hastings 2018; De la Torre and Rivero 2019).

Topographic variables may affect hunting opportunities (Kruuk 2006), but more likely they are also correlated with other variables such as distribution of humans,

protected areas, and land/vegetation cover that are more directly correlated with factors affecting jaguar distribution. Still, elevation may be widely used by researchers who can easily get this information without advanced training in geographic information technologies.

Even though some carnivores can partially fulfill their nutritional water requirements with prey, hunting places near water could increase predator encounters, especially in seasonal environments (Sirot et al. 2016). Distance to water is a commonly used metric, likely also because researchers can easily get this information without advanced training. Though we did not find evidence suggesting fresh water as driver of jaguar density at local scale, we hypothesize in seasonal ecosystems water might be related to prey and therefore to higher jaguar densities.

Distance to beach was identified once as a significant variable in a place where nesting sea turtles are seasonally abundant, and thus a variable reflecting peaks of prey availability (Carrillo et al. 2009). This suggests that modeling considerations should take into account the special circumstances of the study site.

Many variables were not identified as significant, though it seems like they could be important constrainers of jaguar distribution. It is likely that the metrics assessed are constrained by a variety of issues, including the types of variables available (Jędrzejewski et al. 2017; Silva et al. 2018; Anile et al. 2020) or the lack of ease to build them (Colchero et al. 2010; Petracca 2010). Also, variables cannot always be based on or derived for specific effects for which human activities or environmental conditions limit or enhance jaguar presence. Finally, some assessments are constrained by the kinds and/or amounts of data used in modeling. Sample sizes may limit, for example, assessment of sex-, age-, or behavior-specific influences on distribution.

Elucidating jaguar occurrence within its range with a limited number of meaningful predictors is not an easy task. Although jaguars can persist in a wide variety of ecosystems, if the set of variables selected are not causally related to jaguar density at a local scale, occurrence data likely does not directly infer density or population trends, hence species occurrence does not mean that jaguar populations are thriving. Because even the simple use of photo rates of jaguars does not seem to correlate well with jaguar density (Maffei et al. 2011), more focus on monitoring factors directly influencing density is warranted.

Conclusion

Thoughtful assessment of variables potentially affecting jaguar distribution should direct researchers to better identify and then quantify specific casual factors affecting jaguar distribution, rather than simply describe it, especially in terms of jaguar reproduction, survival, and dispersal. Habitat descriptors are useful in understanding a species' niche (Hutchinson 1957), and habitat quality is often inferred from the distribution of species (McLoughlin et al. 2010). Habitat use patterns may provide a link to population dynamics (Bernal-Escobar et al. 2015; Boyce et al. 2016;

Morato et al. 2019), but such links have not been well identified for jaguars. So, even though linking demographic rates to habitat use is logistically and financially challenging, doing so will provide the demonstrated relationships that are needed to best conserve jaguar populations into the future. Jaguar habitat modeling provides a plethora of hypotheses to test, and demographic data will unveil the mechanisms providing for jaguar population viability.

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References

Anile S, Greenspan E, Nielsen C (2020) Determinants of jaguar occupancy at the northern range edge. Mammal Research 65(4): 667–677. https://doi.org/10.1007/s13364-020-00511-0

Arroyo-Arce S, Guilder J, Salom-Pérez R (2014) Habitat features influencing jaguar *Panthera onca* (Carnivora: Felidae) occupancy in Tortuguero National Park, Costa Rica. Revista de Biología Tropical 62(4): 1449–1458. https://doi.org/10.15517/rbt.v62i4.13314

Ashcroft M, French KO, Chisholm LA (2011) An evaluation of environmental factors affecting species distributions. Ecological Modelling 222(3): 524–531. https://doi.org/10.1016/j.ecolmodel.2010.10.003

Astete S, Marinho-Filho J, Kain G, Penido B, Zimbres R, Sollmann R, Jácomo ATA, Tórres NM, Silveira L (2017a) Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. Journal of Arid Environments 146: 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005

Astete S, Marinho-Filho J, Machado RB, Zimbres B, Jácomo ATA, Sollmann R, Tôrres NM, Silveira L (2017b) Living in extreme environments: Modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat. Journal of Mammalogy 98: 464–474. https://doi.org/10.1093/jmammal/gyw184

Ávila-Nájera DM, Lazcano-Barrero M, Chavez C, Pérez-Elizalde S, Tigar B, Mendoza GD (2019) Uso de habitat del jaguar (*Panthera onca*) en un bosque tropical del norte de Quintana Roo, México. Revista Mexicana de Biodiversidad 90: e902186. https://doi.org/10.22201/ib.20078706e.2019.90.2186

Ávila-Nájera D, Chavéz M, Pérez-Elizalde S, Palacios-Pérez J, Tigar B (2020) Coexistence of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a tropical forest in southeastern Mexico. Animal Biodiversity and Conservation 43(1): 55–66. https://doi.org/10.32800/abc.2020.43.0055

Azevedo FCC, Murray DL (2007) Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. Biological Conservation 137(3): 391–402. https://doi.org/10.1016/j.biocon.2007.02.022

Bernal-Escobar A, Payan E, Cordovez JM (2015) Sex dependent spatially explicit stochastic dispersal modeling as a framework for the study of jaguar conservation and management in South America. Ecological Modelling 299: 40–50. https://doi.org/10.1016/j.ecolmodel.2014.12.002

Bitetti MSD, Angelo CDD, Blanco YED, Paviolo A (2010) Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica 36(4): 403–412. https://doi.org/10.1016/j.actao.2010.04.001

Booker H (2016) The application of occupancy modeling to evaluate the determinants of distribution of jaguars (*Panthera onca*), pumas (*Puma concolor*) and valued prey species in a protected area. Dissertation, University of Waterloo.

Borrego CS (2015) Differential effects of habitat on the occupancy of jaguars, pumas and sympatric carnivores in Sonora, Mexico. Dissertation, Washington State University.

Boyce M, Jhonson C, Merill E, Nielsen S, Solberg E, Moorter B (2016) Can habitat selection predict abundance? Journal of Animal Ecology 85(1): 11–20. https://doi.org/10.1111/1365-2656.12359

Boydston EE, González CA (2005) Sexual differentiation in the distribution potential of northern jaguars (*Panthera onca*). In: Gottfried GJ, Gebow Z, Brooke S, Eskew LG, Edminster CB (Eds) Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II. Proc. RMRS-P-36, Colorado, 51–56.

Carrillo E, Fuller TK, Sáenz JC (2009) Jaguar (*Panthera onca*) hunting activity: Effects of prey distribution and availability. Journal of Tropical Ecology 25(5): 563–567. https://doi.org/10.1017/S0266467409990137

Carvalho Jr EA, Zarco-González MM, Monroy-Vilchis O, Morato RG (2015) Modeling the risk of livestock depredation by jaguar along the Transamazon highway, Brazil. Basic and Applied Ecology 16(5): 413–419. https://doi.org/10.1016/j.baae.2015.03.005

Cavalcanti SM (2008) Predator-prey relationships and spatial ecology of jaguars in the southern Pantanal, Brazil: Implications for conservation and management. Dissertation, Utah State University.

Ceballos G, Ehrlich P, Soberón J, Salazar I, Fay J (2005) Global mammal conservation: What must we manage? Science 109(5734): 603–609. https://doi.org/10.1126/science.1114015

Cobucci-Cerqueira R, Rodrigues de Rivera O, Jaeger J, Grilo C (2021) Direct and indirect effects of roads on space use by jaguars in Brazil. Scientific Reports 11: 22617. https://doi.org/10.1038/s41598-021-01936-6

Colchero F, Conde DA, Manterola C, Chávez C, Rivera A, Ceballos G (2010) Jaguars on the move: Modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. Animal Conservation 14(2): 158–166. https://doi.org/10.1111/j.1469-1795.2010.00406.x

Conde DA, Colchero F, Zarza H, Christensen Jr NL, Sexton JO, Manterola C, Chávez C, Rivera A, Azuara D, Ceballos G (2010) Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation 143(9): 1980–1988. https://doi.org/10.1016/j.biocon.2010.04.049

Craighead K (2019) A multi-scale analysis of jaguar (*Panthera onca*) and puma (*Puma concolor*) habitat selection and conservation in the narrowest section of Panamá. Dissertation, Antioch University.

Cuervo-Robayo AP, Monroy-Vilchis O (2012) Distribución potencial del jaguar *Panthera onca* (Carnivora: Felidae) en Guerrero, Mexico: persistencia de zonas para su conservación. Revista de Biología Tropical 60(3): 1357–1367. https://doi.org/10.15517/rbt.v60i3.1813

Cullen L, Sana DA, Lima F, De Abreu KC, Uezu A (2013) Selection of habitat by the jaguar, *Panthera onca* (Carnivora: Felidae), in the upper Paraná River, Brazil. Zoologia 30(4): 379–387. https://doi.org/10.1590/S1984-46702013000400003

Cuyckens GAE, Perovic PG, Herrán M (2017) Living on the edge: Regional distribution and retracting range of the jaguar (*Panthera onca*). Animal Biodiversity and Conservation 40(1): 71–86. https://doi.org/10.32800/abc.2017.40.0071

Dallas T, Hastings A (2018) Habitat suitability estimated by niche models is largely unrelated to species abundance. Global Ecology and Biogeography 27(12): 1448–1456. https://doi.org/10.1111/geb.12820

Davis ML, Kelly MJ, Stauffer DF (2010) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Animal Conservation 14(1): 56–65. https://doi.org/10.1111/j.1469-1795.2010.00389.x

De la Torre JA, Núñez JM, Medellín RA (2017) Spatial requirements of jaguars and pumas in Southern Mexico. Mammalian Biology 84: 52–60. https://doi.org/10.1016/j.mambio.2017.01.006

De la Torre JA, Rivero M (2019) Insights of the movements of thej in the tropical forests of southern Mexico. In: Reina-Hurtado R (Ed.) Movement Ecology of Neotropical Forest Mammals. Springer Cham, Switzerland, 217–241. https://doi.org/10.1007/978-3-030-03463-4_13

DeMatteo KE, Rinas MA, Zurano JP, Selleski N, Schneider RG, Argüelles CF (2017) Using niche-modelling and species-specific cost analyses to determine a multispecies corridor in a fragmented landscape. PLoS ONE 12(8): e0183648. https://doi.org/10.1371/journal.pone.0183648

Dobbins MT, Steinberg MK, Broadbent EN, Ryan SJ (2017) Habitat use, activity patterns and human interactions with jaguars *Panthera onca* in southern Belize. Oryx 52(2): 276–281. https://doi.org/10.1017/S0030605317000308

Dueñas-López G, Rosas OCR, Chapa-Vargas L, Bender LC, Tarango-Arámbula LA, Martínez-Montoya JF, Alcántara-Carbajal JL (2015) Connectivity among jaguar populations in the Sierra Madre Oriental, México. Therya 6(2): 449–468. https://doi.org/10.12933/therya-15-257

Espinosa S, Celis G, Branch LC (2018) When roads appear jaguars decline: Increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PLoS ONE 13(1): e0189740. https://doi.org/10.1371/journal.pone.0189740

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet. Earth Science 333: 301–306. https://doi.org/10.1126/science.1205106

Fort J (2016) Large Carnivore Occupancy and Human-Wildlife Conflict in Panamá. Dissertation, Southern Illinois University, Illinois.

Fuller TK, Sievert PR (2001) Carnivore demography and the consequences of changes in prey availability. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (Eds) Carnivore Conservation. Cambridge University Press, London, 163–178.

Gese EM, Terletzky PA, Cavalcanti SMC, Neale CMU (2018) Influence of behavioral state, sex, and season on resource selection by jaguars (*Panthera onca*): Always on the prowl? Ecosphere 9(7): e02341. https://doi.org/10.1002/ecs2.2341

Gonzales-Borrajo N, López-Bao JV, Palomares F (2019) Spatial ecology of jaguars, pumas, and ocelots: A review of the state of knowledge. Mammal Review 47(1): 62–85. https://doi.org/10.1111/mam.12081

Guilder J, Barca B, Arroyo-Arce S, Gramajo R, Salom-Pérez R (2015) Jaguars (*Panthera onca*) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle (*Chelonia mydas mydas*) abundance in Tortuguero National Park, Costa Rica. Mammalian Biology 80(2): 65–72. https://doi.org/10.1016/j.mambio.2014.11.005

Gutiérrez-González CE, López-González CA (2017) Jaguar interactions with pumas and prey at the northern edge of jaguars' range. PeerJ 5: e2886. https://doi.org/10.7717/peerj.2886

Harmsen BJ, Foster RJ, Silver SC, Ostro LET, Doncaster C (2009) Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. Journal of Mammalogy 90(3): 612–620. https://doi.org/10.1644/08-MAMM-A-140R.1

Harmsen BJ, Foster RJ, Silver SC, Ostro LET, Doncaster C (2011) Jaguar and puma activity patterns in relation to their main prey. Mammalian Biology 76(3): 320–324. https://doi.org/10.1016/j.mambio.2010.08.007

Hatten JR, Averill-Murray A, Pelt WEV (2003) A spatial model of potential jaguar habitat in Arizona. The Journal of Wildlife Management 69(3): 1024–1033. https://doi.org/10.2193/0022-541X(2005)069[1024:ASMOPJ]2.0.CO;2

Hidalgo-Mihart M, Contreras-Moreno F, De la Cruz A (2018) Validation of the Calakmul–Laguna de Terminos corridor for jaguars *Panthera onca* in southeastern Mexico. Oryx 52(2): 292–299. https://doi.org/10.1017/S0030605316001083

Hutchinson GE (1957) Concluding remarks. Cold spring harbor symposia on Quantitative Biology 22(0): 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Jędrzejewski WE, Boede E, Abarca M, Sánchez-Mercado A, Ferrer-Paris JR, Lampo M, Velásquez G, Carreño R, Viloria ÁL, Hoogesteijn R, Robinson HS, Stachowicz I, Cerda H, Weisz MM, Barros TR, Rivas GA, Borges G, Molinari J, Lew D, Takiff H, Schmidt K (2017) Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. Biological Conservation 206: 132–142. https://doi.org/10.1016/j.biocon.2016.09.027

Jędrzejewski W, Robinson HS, Abarca M, Zeller K, Velasquez G, Paemelaere E, Goldberg JF, Payan E, Hoogesteijn R, Boede EO, Schmidt K, Lampo M, Viloria ÁL, Carreño R, Robinson N, Lukacs PM, Nowak JJ, Salom-Pérez R, Castañeda F, Boron V, Quigley H (2018) Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – application to the jaguar (*Panthera onca*). PLoS ONE 13(3): e0194719. https://doi.org/10.1371/journal.pone.0194719

Jordan CA, Schank CJ, Urquhart GR, Dans AJ (2016) Terrestrial mammal occupancy in the context of widespread forest loss and a proposed interoceanic canal in Nicaragua's decreasingly remote south Caribbean region. PLoS ONE 11(3): e0151372. https://doi.org/10.1371/journal.pone.0151372

Junior LC, Sana DA, Lima F, Abreu KCD, Uezu A (2013) Selection of habitat by the jaguar, *Panthera onca* (Carnivora: Felidae), in the upper Paraná River, Brazil. Zoologia 30(4): 379–387. https://doi.org/10.1590/S1984-46702013000400003

Karanth U (1995) Estimating tiger populations from camera-trap data using capture-recapture models. Biological Conservation 71(3): 333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Kareiva P, Marvier M (2015) Conservation Science: Balancing the Needs of People and Nature (2nd edn.). Roberts and Company Publishers, Colorado.

Kruuk H (2006) Otters: Ecology, Behaviour, and Conservation. Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780198565871.001.0001

López C, Miller B (2002) Do jaguars (*Panthera onca*) depend on large prey? Western North American Naturalist 62: 218–222.

Luja VH, Navarro CJ, Covarrubias LAT, Hernández MC, Chan ILV (2017) Small protected areas as stepping-stones for jaguars in western Mexico. Tropical Conservation Science 10: 1–8. https://doi.org/10.1177/1940082917717051

MacBride Jr RT, Thompson J (2018) Space use and movement of jaguar (*Panthera onca*) in western Paraguay. Mammalia 82(6): 540–549. https://doi.org/10.1515/mammalia-2017-0040

MacGarigal K, Wan H, Zellerm K, Timm B, Cushman S (2016) Multi-scale habitat selection modeling: A review and outlook. Landscape Ecology 31(6): 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

Mackenzie DI, Nichols JD (2004) Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27: 461–467.

Mackenzie D, Nichols J, Royle J, Pollock K, Bailey L, Hines J (2017) Occupancy Estimation and Modeling (2nd edn.). Academic Press, New York. https://doi.org/10.1016/B978-0-12-407197-1.00003-X

Maffei L, Noss AJ, Silver SC, Kelly MJ (2011) Abundance/density case study: Jaguars in the Americas. In: O'Connell AF, Nickols JD, Karanth KU (Eds) Camera Traps in Animal Ecology. Springer, Tokyo, 119–144. https://doi.org/10.1007/978-4-431-99495-4_8

Manly B, McDonald L, Thomas L, MacDonald TL, Erickson WP (2002) Resource Selection by Animals (2nd edn.). Kluwer Academic Publishers, London.

McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL (2010) Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79(1): 4–12. https://doi.org/10.1111/j.1365-2656.2009.01613.x

Michalski LJ, Norris D, Oliveira TGD, Michalski F (2015) Ecological relationships of meso-scale distribution in 25 neotropical vertebrate species. PLoS ONE 10(5): e0126114. https://doi.org/10.1371/journal.pone.0126114

Montanarin A (2020) Efeito de variáveis ambientais e antrópicas na seleção de habitat por machos e fêmeas de onça-pintada (*Panthera onca*) em uma área de várzea do médio solimões. Dissertation, Instituto Nacional de Pesquisas da Amazônia.

Morato RG, Ferraz K, De Paula RG, Campos CB (2014) Identification of priority conservation areas and potential corridors for jaguars in the Caatinga biome, Brazil. PLoS ONE 9(4): e92950. https://doi.org/10.1371/journal.pone.0092950

Morato RG, Stabach JA, Fleming CH, Calabrese JM, De Paula RC, Ferraz KMPM, Kantek DLZ, Miyazaki SS, Pereira TDC, Araujo GR, Paviolo A, De Angelo C, Di Bitetti MS, Cruz P, Lima F, Cullen L, Sana DA, Ramalho EE, Carvalho MM, Soares FHS, Zimbres B, Silva MX, Moraes MDF, Vogliotti A, May JA, Haberfeld M, Rampim L, Sartorello L, Ribeiro MC, Leimgruber P (2016) Space use and movement of a neotropical top predator: The endangered jaguar. PLoS ONE 11(12): e0168176. https://doi.org/10.1371/journal.pone.0168176

Morato RG, Connette GM, Stabach JA, De Paula RC, Ferrazc K, Kanteke D, Miyazaki SS, Pereira TDC, Silva LC, Paviolo A, De Angelo C, Di Bitetti MS, Cruz P, Lima F, Cullen L, Sana DA , Ramalho EE, Carvalho MM, da Silva MX, Moraes MDF, Vogliotti A, May Jr JA, Haberfeld M, Rampim L, Sartorello L, Araujo GR, Wittemyer G, Ribeiro MC, Leimgruber P (2019) Resource selection in an apex predator and variation in response to local landscape characteristics. Biological Conservation 228: 233–240. https://doi.org/10.1016/j.biocon.2018.10.022

Morrison L, Marcot BG, Mannan W (2006) Wildlife-habitat relationships: concepts and applications. NCASI Technical Bulletin, 1–69. https://www.ncasi.org/wp-content/uploads/2019/02/tb909.pdf

Olsoy PJ, Zeller KA, Hicke JA, Quigley HB, Rabinowitz AR, Thornton DH (2016) Quantifying the effects of deforestation and fragmentation on a range-wide conservation plan for jaguars. Biological Conservation 203: 8–16. https://doi.org/10.1016/j.biocon.2016.08.037

Palmeirim A, Gibson K (2021) Impacts of hydropower on the habitat of jaguars and tigers. Communications Biology 4(1): e1358. https://doi.org/10.1038/s42003-021-02878-5

Paschoaletto K, De Barros Ferraz S (2012) Species distribution modeling for conservation purposes. Natureza & Conservação 10(2): 214–220. https://doi.org/10.4322/natcon.2012.032

Petracca L (2010) Use of site occupancy modeling to delineate a jaguar corridor in southern Belize. Dissertation, Duke University.

Petracca L, Ramírez-Bravo O, Hernández-Santín L (2013) Occupancy estimation of jaguar *Panthera onca* to assess the value of east-central Mexico as a jaguar corridor. Oryx 48(1): 133–140. https://doi.org/10.1017/S0030605313000069

Phillips S, Anderson R, Dudík M, Schapire R, Blair M (2017) Opening the black box: An open-source release of Maxent. Ecography 40(7): 887–893. https://doi.org/10.1111/ecog.03049

Portugal M, Morato R, Barrios-Ferraz K, Guimares-Rodrigues F (2019) Priority areas for jaguar *Panthera onca* conservation in the Cerrado. Oryx 53: 1–12.

Punchi-Manage R, Getzin S, Wiegand T, Kanagaraj R, Savitri Gunatilleke CV, Nimal Gunatilleke IAU, Wiegand K, Huth A (2013) Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. Journal of Ecology 101(1): 149–160. https://doi.org/10.1111/1365-2745.12017

Quigley H, Foster R, Petracca L, Payan E, Salom R, Harmsen B (2017) *Panthera onca* (errata version published in 2018). The IUCN Red List of Threatened Species 2017. https://www.iucnredlist.org/

Quiñones A, Fuller TK, Randhir T (2018) A review of otter distribution modeling approach, scale and metrics. IUCN Otter Specialist Group Bulletin 35: 93–122.
Rabinowitz A, Nottingham BG (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. Journal of Zoology (London, England) 210(1): 149–159. https://doi.org/10.1111/j.1469-7998.1986.tb03627.x
Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biological Conservation 143(4): 939–945. https://doi.org/10.1016/j.biocon.2010.01.002
Ripple W, Beschta L, Painter E (2015) Trophic cascades from wolves to alders in Yellowstone. Forest Ecology and Management 354: 254–260. https://doi.org/10.1016/j.foreco.2015.06.007
Rodríguez-Soto C, Monroy-Vilchis O, Maiorano L, Boitani L, Faller JC, Briones MA, Núñez R, Rosas-Rosas O, Ceballos G, Falcucci A (2011) Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: Identification of priority areas for conservation. Diversity & Distributions 17(2): 350–361. https://doi.org/10.1111/j.1472-4642.2010.00740.x
Romero-Muñoz A, Torres R, Noss A, Giordano AJ, Quiroga V, Thompson J, Baumann M, Altrichter M, McBride Jr R, Velilla M, Arispe R, Kuemmerle T (2018) Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. Diversity & Distributions 25(2): 176–190. https://doi.org/10.1111/ddi.12843
Salom R, Carrillo E, Sáenz J (2007) Critical condition of the jaguar (*Panthera onca*) population in Corcovado National Park, Costa Rica. Oryx 41(1): 51–56. https://doi.org/10.1017/S0030605307001615
Sanderson EW, Redford KH, Chetkiewicz CL, Medellín RA, Rabinowitz A, Robinson J, Taber AB (2002) Planning to save a species: The jaguar as a model. Conservation Biology 16(1): 58–72. https://doi.org/10.1046/j.1523-1739.2002.00352.x
Sanderson EW, Fisher K, Peters R, Beckmann J, Bird B, Bradley C, Bravo JC, Grigione MM, Hatten JR, Lopez González CA, Menke K, Miller JRB, Miller PS, Mormorunni C, Robinson MJ, Thomas RE, Wilcox S (2022) A systematic review of potential habitat suitability for the jaguar *Panthera onca* in central Arizona and New Mexico. Oryx 56(1): 116–127. https://doi.org/10.1017/S0030605320000459
Sandoval I, Carrillo E, Saenz J (2011) Modelo de hábitat potencial para el jaguar, *Panthera onca* (Carnivora:Felidae), en la peninsula de Osa Costa Rica. Costa Rica. Brenesia 76: 90–96.
Schaller GB, Crawshaw PG (1980) Movement patterns of jaguar. Biotropica 12(3): e161. https://doi.org/10.2307/2387967
Seymour L (1989) *Panthera onca*. Mammalian Species 340(340): 1–9. https://doi.org/10.2307/3504096
Silva M, Paviolo A, Tambosi LR, Pardini R (2018) Effectiveness of protected areas for biodiversity conservation: Mammal occupancy patterns in the Iguaçu National Park, Brazil. Journal for Nature Conservation 41: 51–62. https://doi.org/10.1016/j.jnc.2017.11.001
Silveira L, Sollmann R, Jácomo ATA, Filho J, Tôrres N (2014) The potential for large-scale wildlife corridors between protected areas in Brazil using the jaguar as a model species. Landscape Ecology 29(7): 1213–1223. https://doi.org/10.1007/s10980-014-0057-4
Silver S, Ostro L, Marsh L, Maffei L, Noss A, Kelly M, Ayala G (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38(2): 148–154. https://doi.org/10.1017/S0030605304000286

Sirot E, Renaud PC, Pays O (2016) How competition and predation shape patterns of waterhole use by herbivores in arid ecosystems. Animal Behaviour 118: 19–26. https://doi.org/10.1016/j.anbehav.2016.05.021

Sollmann R (2011) Ecology and conservation of the jaguar (*Panthera onca*) in the Cerrado grasslands of central Brazil. Dissertation, Freie Universität Berlin, Berlin.

Sollmann R, Furtado M, Hofer H, Jácomo AT, Tôrres NM, Silveira L (2012) Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammalian Biology 77(1): 41–46. https://doi.org/10.1016/j.mambio.2011.06.011

Souza J, Silva R, Gonçalves Jardim M, Markwith S (2017) Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. Biological Conservation 217: 349–357. https://doi.org/10.1016/j.biocon.2017.11.019

Sunquist M, Sunquist F (2002) Wild Cats of the World. University of Chicago Press, USA. https://doi.org/10.7208/chicago/9780226518237.001.0001

Thompson J, Velilla M (2017) Modeling the effects of deforestation on the connectivity of jaguar *Panthera onca* populations at the southern extent of the species' range. Endangered Species Research 34: 109–121. https://doi.org/10.3354/esr00840

Thompson J, Martínez C, Quigley H (2020) Anthropogenic factors disproportionately affect the occurrence and potential population connectivity of the Neotropic's apex predator: The jaguar at the southwestern extent of its distribution. Global Ecology and Conservation 24: e01356. https://doi.org/10.1016/j.gecco.2020.e01356

Thompson J, Morato RG, Niebuhr BB, Bejarano-Alegre V, Oshima JEF, de Barros AE, Paviolo A, de la Torre JA, Lima F, McBride Jr RT, de Paula RC, Cullen Jr L, Silveira L, Kantek DLZ, Ramalho EE, Maranhão L, Haberfeld M, Sana DA, Medellin RA, Carrillo E, Montalvo VH, Monroy-Vilchis O, Cruz P, Jacomo ATA, Alves GB, Cassaigne I, Thompson R, Sáenz-Bolaños C, Cruz JC, Alfaro LD, Hagnauer I, da Silva MX, Vogliotti A, Moraes MFD, Miyazaki SS, Araujo GR, da Silva LC, Leuzinger L, Carvalho MM, Rampim L, Sartorello L, Quigley H, Tortato FR, Hoogesteijn R, Crawshaw Jr PG, Devlin AL, May Jr JA, Powell GVN, Tobler MW, Carrillo-Percastegui SE, Payán E, Azevedo FCC, Concone HVB, Quiroga VA, Costa SA, Arrabal JP, Vanderhoeven E, Di Blanco YE, Lopes AMC, Ribeiro MC (2021) Environmental and anthropogenic factors synergistically affect space use of jaguars. Current Biology 31(15): 1–10. https://doi.org/10.1016/j.cub.2021.06.029

Thornton D, Zeller K, Rondinini C, Boitani L, Crooks KR, Burdett C, Rabinowitz A, Quigley H (2016) Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). Ecological Applications 26(4): 1112–1124. https://doi.org/10.1890/15-0602

Torres C (2021) Assessing the connectivity for the jaguar (*Panthera onca*) in the United States-Mexico border ecoregions using species distribution modeling and factorial least cost path analysis. Dissertation, University of Southern California.

Torres NM, De Marco P, Diniz Filho J, Silveira L (2008) Jaguar distribution in Brazil: Past, present and future. Cat News 4: 4–8. https://doi.org/10.1098/rsbl.2008.0210

Torres NM, Marco PD, Santos T, Silveira L, Jácomo ATA, Diniz-Filho J (2012) Can species distribution modelling provide estimates of population densities? A case study

with jaguars in the Neotropics. Diversity & Distributions 18(6): 615–627. https://doi.org/10.1111/j.1472-4642.2012.00892.x

Watkins A, Noble J, Foster R, Harmsen B, Doncaster C (2015) A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecological Modelling 306: 268–277. https://doi.org/10.1016/j.ecolmodel.2014.10.038

Weckel M, Giuliano W, Silver S (2006) Jaguar (*Panthera onca*) feeding ecology: Distribution of predator and prey through time and space. Journal of Zoology (London, England) 270(1): 25–30. https://doi.org/10.1111/j.1469-7998.2006.00106.x

Zárrate-Charry DA, Massey AL, González-Maya JF, Betts MG (2018) Multi-criteria spatial identification of carnivore conservation areas under data scarcity and conflict: A jaguar case study in Sierra Nevada de Santa Marta, Colombia. Biodiversity and Conservation 27(13): 3373–3392. https://doi.org/10.1007/s10531-018-1605-z

Zeilhofer P, Cezar A, Tôrres NM, Jácomo ATA, Silveira L (2014) Jaguar *Panthera onca* habitat modeling in landscapes facing high land-use transformation pressure-findings from Mato Grosso, Brazil. Biotropica 46(1): 98–105. https://doi.org/10.1111/btp.12074

Zeller KA, Rabinowitz A (2011) Using geographic information systems for range-wide species conservation planning. In: Dawsen CJ (Ed.) Geographic Information Systems. Nova Publishers, New York, 21 pp.

Supplementary material 1

List of manuscripts and variables used in this analysis

Authors: Víctor H. Montalvo, Carolina Sáenz-Bolaños, Eduardo Carrillo, Todd K. Fuller

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Link: https://doi.org/10.3897/neotropical.18.e98437.suppl1

Supplementary material 2

Variables summary

Authors: Víctor H. Montalvo, Carolina Sáenz-Bolaños, Eduardo Carrillo, Todd K. Fuller

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